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EVOLUTION AND DICHROMATISM IN THE GENUS MEGASCOPS.

By E. M. Hasbrouck.

INTRODUCTION.

The subject of Dichromatism has ever been a stumbling-block to scientific research, and from the time of its earliest admittance into zoological discussion, has been without apparent cause and without explanation. Few, if any, theories have been published as to what it really is, or as to the possible influence governing it, while any theories that have been advanced stand without proof of their correctness; a new theory, therefore, cannot be considered as conflicting with any *settled* doctrine upon the subject. When we find a peculiarity common to all forms of animal life, it becomes apparent that if thoroughly understood in one form, a flood of light will be thrown upon the same perplexing problem affecting the rest of the animal kingdom.

In attempting to explain the causes and effects of dichromatism in the Screech Owl, no stone has been left unturned to prove the correctness of the views herein set forth. The writer has labored lovingly and patiently, following a course of reasoning which he believes to be correct, and in submitting his work and its results to fellow-workers would ask for it their kindly consideration. The collection of the necessary data has been an extremely difficult task, and more information is still desirable from certain localities, although sufficient has been received to make possible the construction of a comparatively accurate map of the color distribution. It is a lamentable fact that scientific observers of bird life are exceedingly scarce in the southern states and in the lower part of the Mississippi Valley. The data obtained from these regions, although to a certain extent more scanty than could be desired, has been used to the best possible advantage. In obtaining information, copies of the following circular letter were sent out by the National Museum, and the matter received in reply was turned over to me for study and investigation, together with the privilege of preparing the results for publication.

UNITED STATES NATIONAL MUSEUM
UNDER DIRECTION OF
THE SMITHSONIAN INSTITUTION.

Dear Sir:

The National Museum is engaged in a systematic investigation of the color-phases of the Screech Owl (*Megascops asio*), with the view of determining the relative abundance of the red and gray plumages in different parts of the country, the plumage of the young, produced by parents of known character as to plumage, and the other related questions.

In order that the investigation may be as thorough as possible, assistance in the matter is requested; and if you can give information on the subject, your kind co-operation will be much appreciated.

Should you favor us with any information on the subject, please arrange the data in the following order:

(1) Name your locality, including County and State.

(2) State about how many specimens have come under your notice, and how many of them were in the gray plumage.

(3) If you have obtained or observed a pair of old birds with their young, state the character of plumage of the former (whether both red, both gray, or one red and one gray—and if the latter, the sex represented by each phase), and also the plumage of the young.

The above are the principal points upon which information is desired, but any additional memoranda will be very acceptable.

Yours truly,
ROBERT RIDGWAY,
Curator, Department of Birds.

In conclusion I wish to express my gratitude to Professor G. Brown Goode, Assist. Secretary of the Smithsonian, and Mr. Robert Ridgway, Curator of Birds, who rendered every assistance and courtesy in their power; while to all who responded to the request for information, without which the task would have been impossible, is due the sincere thanks of The Author

PART I.

RELATIONSHIP OF DICHROMATISM TO EVOLUTION.

So universally adopted has the theory of evolution become, that it scarcely seems necessary to refer to it as forming the foundation of the theory here advanced, regarding the dichromatic phases of the common Screech Owl (*Megascops asio*).

"In the Systema Naturæ (Vol. I, 12 Ed., 1766, p. 132), the Red Owl is first described by Linnæus under the name of *Strix asio.* Twenty-two years later (1788) Gmelin described (Systema Naturæ, Vol. I, 13 Ed., p. 289) the Mottled Owl as *Strix nævia.* In 1812, in the fifth volume of his American Ornithology, Alexander Wilson re-describes the two under the same names, also as distinct species, and not until 1828 does it appear to have been publicly hinted that the two were really identical, when Prince C. L. Bonaparte united them, he considering the red bird as the young, and the gray the old. Audubon, in 1832, sustains this view; one of the red birds he figures as the young, being one he reared from a fledgling. Nuttall, a few years later, supports the same view. In 1837, Dr. S. Cabot, Jr. (Journ. Bost. Soc. Nat. Hist., Vol. II, p. 126), while considering the two birds identical in species, reverses the order, making the red plumage the old and the gray the young, and in confirmation of his views exhibited as seeming conclusive evidence, an old red bird which he shot while in the act of feeding some gray young, which he also exhibited. In July of the same year, Dr. Ezra Michener, in a paper (Phila. Acad. Nat. Sci., Vol. 7, p. 53) entitled, *A few Facts, in Relation to the Identity of the Red and Mottled Owl,* states that he had seen young Screech Owls, accompanied by their parents, after leaving the nest, of both red and gray colors, the parents being always of the same color as the young. "The conclusion is, therefore," he says, "evident, either that the color of both old and young is variable or uncertain, or that they are specifically distinct." The latter opinion he adopts, ignoring the then sole known case of different colors in the young and parent exhibited by Dr. Cabot, very positively concluding that there are *two* species, and that Wilson was right.

Dr. P. R. Hoy, in his *Notes on the Birds of Wisconsin* (Proc. Phil. Acad. Nat. Sci., 1853, Vol. 6), gives them as two distinct species, while Cassin, in his various papers on the owls, adopts the conclusion of Bonaparte; considering them as one species, and the gray the adult."[1]

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[1] Am. Nat., II, 1866, 327-328.

Again, Dr. W. Wood (Am. Nat., Vol. II, 1868, p. 371), mentions two cases:—the one, a Mottled Owl, taken from the nest with one young, neither of which had a red mark on them; the other, a Red Owl, taken with four young, all red. His deductions are, that there are two adults, one red without a gray feather, the other gray without the slightest trace of red; also, that there are young of each before they are able to fly, one gray and white without a red feather, the other with a reddish tinge to all the feathers. These facts he is unable to reconcile, unless, as he says, "It is admitted that the color of the plumage is either 'vaiiable or uncertain,' or else there are two distinct species as described by Wilson."

The whole is admirably summarized and described in Baird, Brewer and Ridgway (Vol. III, 1874, p. 51), in the following words, "That these two very different plumages are entirely independent of age, sex or season, and that they are purely individual there can be no doubt, since in one nest there may often be found both red and gray young ones, while their parents may be either both red or both gray, the male red and the female gray, or *vice versa.* Occasionally specimens are exactly intermediate between these two plumages, it being difficult to decide which predominates."

This difference in plumage has been termed Dichromatism, and while a hundred and twenty-five years have succeeded in establishing the fact that the red and gray screech owls are one and the same species, no satisfactory theory known to the writer has been advanced as to what dichromatism is due in this case or as to the possible causes governing it.

Naturally enough, this is far from satisfactory, while the opinions of various authors just quoted, and which comprise the most of what has been written upon the subject, tend but to raise innumerable queries for which there appear to be no satisfactory answers. Why, for instance, is the gray form dominant in one part of the country and the red in another? Why are both forms equally common in a third? Why is the red phase peculiar to the eastern members of the genus, while in the western forms it is unknown? Above all, why, at the northern boundary of *asio* proper, is the red form entirely

PLATE XIII.

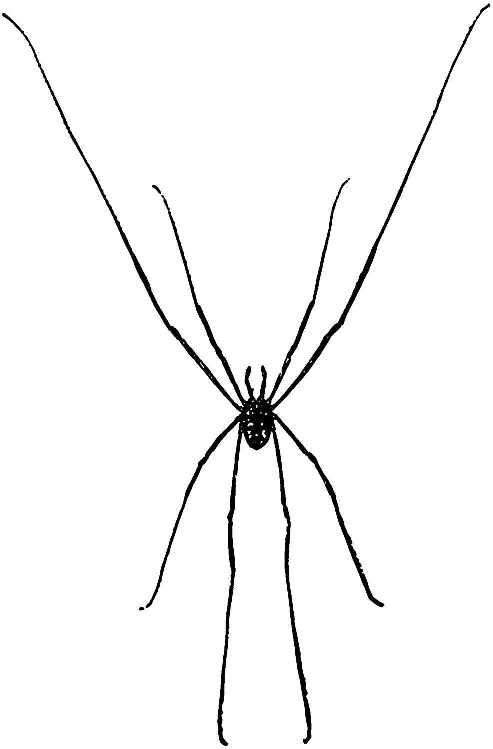

Fig. 1.

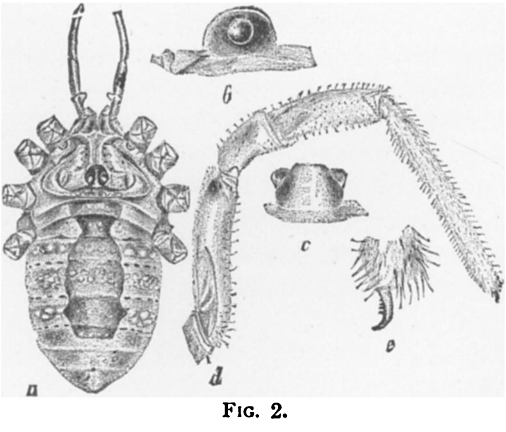

Fig. 2.

Liobunum ventricosum hyemale Weed. Immature.

absent, while at the southern limit it is greatly in the majority? These and many other questions of equal importance present themselves, and but confuse and leave the reader more than ever in the dark.

While collecting screech owls in the District of Columbia during the winter of 1890–91, these questions arose very forcibly, and upon investigating, I found that while the matter was apparently settled to the satisfaction of ornithologists, as regards the identity of the two forms, nothing further appeared to be known about it. Further investigation showed that dichromatism is principally confined to the typical form of *Megascops asio*, appearing but slightly in the Florida form (*Megascops a. floridanus*), and barely reaching the Texan subspecies, *mccallii*. The remaining members of the group, four in number,[1] remaining true to their normal color.[2]

Three phases of plumage were clearly defined—the red, the gray, and the intermediate (the last less frequently seen than the others). Three distinct phases, represented indiscriminately by individuals of one species, regardless of age, sex or season! Such an unusual circumstance that the possibility of some great and important change gradually taking place at once suggested itself, which has been proved to be in reality the case.

An attempt will be made to show, first, that while the red, the gray and the intermediate phases are at present but individual variations of the same species—the gray was the ancestral stock; second, that from the gray bird has evolved the red, which at some future time will be a recognized sub-species with a range peculiar to itself, and thus dichromatism is one step in the evolution of the Screech Owl, while the various phases exhibited are the transitorial stages of development of one species from another; third, that this condition of affairs is influenced by four powerful factors (two of which temperature and humidity, are dominant powers in geographic distribution), the most potent of which is temperature; fourth, that the *predominating* distribution of the respective colors is largely confined to the faunal divisions of the Eastern United States, and as such is approaching the sub-specific differentiation of the two phases; lastly, that the Darwinian theory of 'Reproduction with variation and the survival of the fittest,' is well exemplified in our common little *Megascops asio.*

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[1] Three sub-species recently described by Brewster (Auk, Vol. VIII, 1891, 139–144) would make the number seven, but these are not as yet admitted to the check list.

[2] *M. a. kennicottii* exhibits a dichromatic phase, but it is a decided dark brown, and not a reddish phase, and is not included in the present treatise.

The Screech Owl has been made the subject of investigation simply because it offers one of the best known examples of dichromatism: if explained and disposed of in one case, much light will be thrown upon the same problem relating to many forms of animal life.

To begin with, a short description of the young, together with the manner of attaining the adult plumage of both phases, may be of service to many not thoroughly acquainted with the species. When first hatched they are covered with pure white down, which in a week or ten days begins to show faint traces of transverse dusky bars. At the age of four weeks they are fully barred with gray and white alternately, which markings they retain until the appearance of the first full plumage. As a usual thing, those destined to be red assume a rufous cast in the down shortly before the appearance of the feathers, but this is not always the case, as instances are known where the first intimation of red was the appearance of a rufous feather pushing its way through the gray or mottled down. Such instances, however, are rare, and but few are known to the writer. At the period when feathers first appear, the future color of the young bird is settled beyond a doubt; both the gray and the red birds rapidly attain their mantle, and the colors once assumed are never changed. Much confusion has arisen from the fact that some observers apparently make no distinction between the bird in the gray or mottled down and the gray or mottled plumage and upon the appearance of the red feathers through the gray down, the assertion has been made that the gray feathers changed to red. The gray birds, on the other hand, attain their plumage at precisely the same time and in the same manner as the reds, only that their feathers are gray instead of rufous. If the above simple facts are borne in mind, no trouble need be experienced in undertanding the appearance of the two plumages.

The first step in the work was to ascertain the relative proportion of the red and gray phase in every section of the area covered by the *asio* group of *Megascops* affected by dichromatism. For this purpose nearly one thousand copies of the circular letter referred to in the introduction, were sent to the ornithologists distributed over this territory. Over two hundred replies were received, a few of which failed to be sufficiently explicit to make their contents available, but enough were obtained to compile in a reasonably accurate manner the map showing the distribution of the two color phases (map 2).

On the northern border of the range of *Megascops asio* where gray is the only form known (see map 2), correspondents from southern Ontario state that at occasional rare intervals a red specimen has been taken *in the spring*; all these birds were taken close to Lakes Erie and Ontario—while at Toronto, one pair composed of a gray and red have been known to breed, which necessitates considering the red phase in Ontario. McInraith states that the species is migratory there, to a certain extent, and it is probable that some of the red birds may be chance visitors that have come north with others. With this exception the gray belt is unbroken from Picton, Nova Scotia, through New Brunswick; northern Maine, New Hampshire, Vermont and New York; the southern part of Quebec and Ontario; northern Michigan and Wisconsin; a strip through central Minnesota, thence south-westward across Dakota and most of Nebraska, and ending in a long point near Leavenworth, Kansas. On the south this gray belt is somewhat broken as shown on map 2; in the future more complete data may show it as unbroken here from east to west as it is on the north. Beginning at a point near St. Augustine, in Florida, it encompasses nearly the whole of that state and much of the range of the Florida form, *Megascops a. floridanus*; runs northward and westward to Eufaula in

Alabama, and terminates near Mobile (this terminal point is arbitrary); while in Texas it is resumed in the southwestern portion of the range of *mccallii*.[3]

Next to this belt comes that wherein both phases occur, but where the gray predominates. It begins near Belfast, Maine, follows the exclusive gray belt with irregular outline to its termination in northern Kansas, and continues southward in a broad belt into Louisiana, where it is a question whether or not it becomes broken at New Orleans. Immediately north of New Orleans it begins again at Mandeville, La. (based on specimens in Am. Museum), and continues eastward to the coast in the neighborhood of Savannah. In its northern half it sends a long arm southward, through eastern Massachusetts, into central Rhode Island and Connecticut, again in Western Pennsylvania, it reaches in a narrow strip far down the Alleghanies into Virginia and West Virginia, terminating near latitude 37°, covers practically the whole of Ohio, with a good share of Indiana, and continues thence to Leavenworth, Kansas, the delta of the Mississippi, and to the Atlantic.

Within this area lies the region in which both forms occur, but in which *red* largely predominates (which in turn includes the exclusive red areas), and which occupies nearly one-half the area inhabited by *asio* proper. It of course conforms to the outline of the last described belt, and extends along the entire Atlantic coast from New England to Savannah.

Lastly are the two areas where *red* is the exclusive form. The one of considerable size and importance based upon substantial evidence, lies wholly within the Mississippi Valley: the other, a small strip, extends from a little northwest of Oakdale, North Carolina, to Variety Mills, in Virginia, and including Wytheville. At present the grays are apparently unknown from these areas. It has been impossible to examine material from either, and to those who may have the opportunity, I would point out the desirability of collecting all the specimens possible.

[3] The intermediate region is mapped upon very insufficient data, it being next to impossible to learn anything of this territory, but the best has been done that was possible under the circumstances.

The following table shows the data arranged by states, upon which the map (No. 2) of color distribution is based. The original letters had to be consulted in many cases as to the proper placing of the lines marking the several divisions; the table itself shows but two things: the areas where reds or grays are the exclusive form known, and where each predominates in the mixture of the two; the finer distinctions it is of course impossible to show in tabular form.

It will be remembered from quotations at the beginning, that the young produced by parents of different colors were said to be either all red, all gray, or both; that those produced by parents both of which were *red* were the same; this much is true, *but not a single record can be found of the offsprings of a pair of gray birds showing the slightest trace of red.* That the grays invariably breed true even in a region where red is the predominating color, *and where the individuals in question may themselves be the offspring of red parents,* is of itself a strong point in support of the theory that the gray was the ancestral color. Further, taking into consideration that there are certain areas where a red bird is unknown, it is evident that the grays do certainly produce young the color of their parents; and that where we take the red birds over a very large area and find them continually producing gray birds *together* with red, and compare them with the gray birds which *never* produce a red; it would appear that the gray bird was the original stock, and that the red was an offshoot—a branch, so to speak, which, owing to certain climatic conditions, or certain elements in the environment, gave it the supremacy in the struggle for existence, and that the producing of gray birds by red parents is an evident tendency to revert to ancestral characters. Nor is that old maxim in natural history, *natura non facit saltum* to be ignored; that natural selection played and is playing an important part in the matter is evident, else how came that area in which the grays are entirely absent? That the red birds were a 'sport,' or a freak, and suddenly acquired their characters, is not to be supposed for a moment; but on the theory of 'reproduction with variation' and 'natural selection,' I hold that some slight deviation from the parent stock did at one

TABLE SHOWING DATA BY STATES, UPON WHICH MAP OF COLOR DISTRIBUTION IS BASED.

State.	Red.	Gray.	Source of Information.
Alabama.		Eufaula.	E. L. Brown.
Arkansas.	Cerro Gordo.		Chas. A. Strawn.
	Clinton.		Mrs. Lillie Pleas (Oologist, VIII, 1891, 195).
Connecticut.	Portland.		Jno. H. Sage.
		East Hartford.	Willard E. Treat.
Delaware.	Wilmington.		Walter D. Bush.
Florida.		Palatka.	Jas. Sands.
		Thonotosassa.	W. H. Steacy.
		Citronelle.	Wm. H. Jeremiah.
Georgia.		Faceville.	W. B. McDaniel.
Illinois.	Mt. Carmel.		R. Ridgway (Nat. Hist. Surv. Ill., I, 1889, 417.)
	Odin.		C. B. Vandycook.
	Jacksonville.		Chas. W. Tindall.
	Warsaw.		Chas. K. Worthen.
	Rockford.		J. E. Dickinson.
	Glen Ellyn.		B. T. Gault.
Indiana.		Camden	Trans. Ind. Hort. Soc., 1890, 52.
	Terre Haute.		Trans. Ind. Hort. Soc., 1890, 52.
		Dunreith.	C. E. Pleas.
	Richmond.		Mrs. Lillie E. Pleas.
	Indianapolis.		Fletcher M. Noe.
Iowa.	La Porte City.		Geo. D. Peck.
		Sioux City.	Dr. Guy C. Rich.
	Grinnell.		Lynds Jones.
Kansas.	Argentine.		G. E. Stilwell.
		Manhattan.	D. E. Lantz.
Kentucky.		Ellis.	Dr. Louis Watson.
	Morganfield.		C. J. Lemen.
	Garrard Co.		G. V. Young.
	Versailles.		L. O. Pindar.
	Bell.		Carrington C. Bacon.
Louisiana.	New Orleans.		Gustave Kohn.
		Mandeville.	Collection Aus. Mus. Nat. Hist.
Maine.		Bangor.	Harry Merrill.
Maryland & Dist. of Columbia.	Washington.		A. E. Colburn.
	Washington.		Wm. Palmer.
	Washington.		C. W. Richmond.
	Washington.		J. D. Figgins.
	Washington.		E. M. Hasbrouck.
	Sandy Spring.		James P. Stabler.
	Laurel.		Geo. Marshall.
Massachusetts.	North Stoughton		C. A. Rummey.
		Boston.	Wm. Brewster & E. W. Ricker.
	Holyoke.		W. F. Lamb.
	Taunton.		A. C. Bent.
Michigan.	Grand Rapids.		Stewart E. White.
	Kalamazoo.		Morris Gibbs.
		East Saginaw.	Peter Lepp.

STATE.	RED.	GRAY.	SOURCE OF INFORMATION.
Minnesota.	Rochester.		W. D. Hurlbut.
		Lake City.	E. A. Wise.
Mississippi.	Waverly.		G. V. Young.
Missouri.	Fayette.		J. W. Kilpatrick.
		Butler.	Harvey Clark.
		Independence.	Charles W. Tindall.
Nebraska.		Ong.	Joel Nelson.
	London.		Geo. A. Coleman.
New Hampshire.		Milford.	J. P. Melzer.
	Webster.		Charles F. Goodhue (F. & S., VIII, 113).
New Brunswick.		New Castle.	Phillip Cox.
New Jersey.	Morristown.		Specimens in Am. Mus. Nat. Hist.
New York.		Albany.	B. W. Arnold.
		Oneida Co.	B. W. Arnold.
		Lowville.	C. Fred. Boshart.
		Lockport.	J. L. Davison.
		Owego.	J. Alden Loring.
		Binghampton.	Willard N. Clute.
		Port Byron.	E. M. Hasbrouck.
North Carolina.	Oakdale.		Robt. J. Thompson.
	Weaverville.		J. S. Cairns.
	Raleigh.		H. H. & C. S. Brimley.
Nova Scotia.		Pictou (?).	Prof.A.M.McQuarrie & Prof.McCulloch
Ohio.		Ney.	Jno. O. Snyder.
		Hamilton.	Geo. Harbron & Dr. F. W. Langdon.
		Canton.	R. H. Bulley.
	Cincinnati.		John. W. Shorten (Jour. Cin. Soc. Nat. Hist., VIII, 1885, 52).
		Lebanon.	Raymond W. Smith.
		Salineville.	Wm. A. Savage.
Ontario.		Plover Mills.	Robert Elliott.
		Lansdowne.	C. J. Young.
		Yarker.	John Ewart.
		Danville.	Dr. G. A. McCallum.
		Hamilton.	T. McIluraith.
		Bradford.	A. C. Sloam.
		Listowell.	Wm. D. Kells.
		Annan.	A. C. Sloam.
		Ardtrea.	John Blair.
		Toronto.	James R. Thurston.
		Belleville.	James T. Bell.
Pennsylvania.	Philadelphia.		Chas. A. Voelker (Proc. Del. Val. Orn. Club, I, '90-'91, p. 12).
	Williamsport.		August Koch.
		Scranton.	Arthur B. Williams, Jr.
Rhode Island.		Providence.	Chas. E. Doe.
	Pawtucket.		H. A. Cash.
		Providence.	H. A. Cash.
South Carolina.	Mount Pleasant.		Arthur. T. Wayne.
	Beaufort.		Walter Hoxie.
Tennessee.	Duck River.		J. B. Cathey.
	Tazewell.		B. F. Schultz.
Texas.		Giddings.	J. O. Singley.
		San Antonio.	H. P. Attwater.
		Gainesville.	G. H. Ragsdale.

STATE.	RED.	GRAY.	SOURCE OF INFORMATION.
Texas.	Tyler.		W. L. McDaniel.
		Travis Co.	Chas. D. Oldright.
Vermont.		East Berkshire	G. B. Hopkins.
		Strafford.	Chas. P. Collins.
		Lunnenburg.	W. E. Balch.
		Castleton.	A. O. Johnson.
		St. Johnsbury.	Franklin Fairbanks.
Virginia.	Variety Mills.		H. M. Micklem.
	Wytheville.		John B. Barrett, Jr.
		Eagle Rock.	J. T. Paxton.
		New Market.	Geo. M. Neese.
West Virginia.	Charlestown.		B. W. Mitchell.
		French Creek.	Earle A. Brooks.
		White Sulphur Springs.	Thaddeus Surber.
Wisconsin.	Madison.		Chas. F. Carr.
	Madison.		Wisconsin Nat. Vol. I, 188.
	Racine.		Dr. P. R. Hoy.
	Jefferson.		Ludwig Kumlein.
		Pewaukee.	B. F. Goss.

time occur, which in some way better fitted the individual for the struggle for existance. Through countless generations this has been perpetuated by the inter-breeding of those possessing it, in consequence, the grays, as has been seen (see map), have entirely disappeared in at least one portion of the country, and have become extremely rare in others. Many difficulties exist, both in showing the original condition, and in explaining the present state of affairs. In early scientific work, as is well known, no attention whatever was paid to matters of this nature, consequently it is impossible to ascertain the proportion of red and gray birds at a period say four hundred years ago—still, I hope to reason by analogy. As for the possible causes influencing the change, they will be found fully treated in their proper place; at present the theory is either to be proved or disproved.

Assuming that the gray was the ancestral stock, and that the producing of gray birds by red parents is a tendency to revert to ancestral characters, an analogous case will be found in Darwin's own experiments.

As is well known, many of these were performed with pigeons, which proved to be the best subjects, and the following is quoted from the "Origin of Species:"[1]

[1] Origin of Species, pp. 17-19.

"Great as are the differences between the breeds of the pigeon, I am fully convinced that the common opinion of naturalists is correct, namely, that all are descended from the rock pigeon, *Columba livia* * * * * * The rock pigeon is of a slaty blue with white loins, * * The tail has a terminal dark bar, with the outer feathers externally edged at the base with white. The wings have two black bars. * * Now in every one of the domestic breeds, taking thoroughly well bred birds, all the above marks, even to the white edging of the outer tail feathers, sometimes occur perfectly developed. Moreover, when birds belonging to two or more distinct breeds are crossed, none of which are blue or have any of the specified marks, the mongrel offspring are very apt suddenly to acquire these characters." (If this be true of distinct species, how much more is it true of different color phases of the same species). "To give one instance out of several I have observed: I crossed some white fantails, which breed very true, with some black barbs—and it so happens that blue varieties of barbs are so rare that I never heard of an instance in England, and the mongrels were black brown and mottled. I also crossed a barb with a spot, which is a white bird with red tail and red spot on the forehead, and which notoriously breeds very true; the mongrels were dusky and mottled. I then crossed one of the mongrel barb-fantails with a mongrel barb-spot, and they produced a bird of as beautiful a blue color, with the white loins, double black wing bar, and barred and white edged tail feathers, as any wild rock pigeon! We can understand these facts, on the well known principle of reversion to ancestral characters, if all the domestic breeds are descended from the rock pigeon."

Now if this reversion to ancestral characters occurs in breeds so far removed from the parent stock and from each other—how much more is it reasonable to suppose that a color phase of the screech owl, when found continually producing gray birds, while gray birds produce grays alone—is but a repetition only between birds more closely related, of the same performance?

(*To be continued.*)